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THE ADAPTATIONS OF THE PRIMATES

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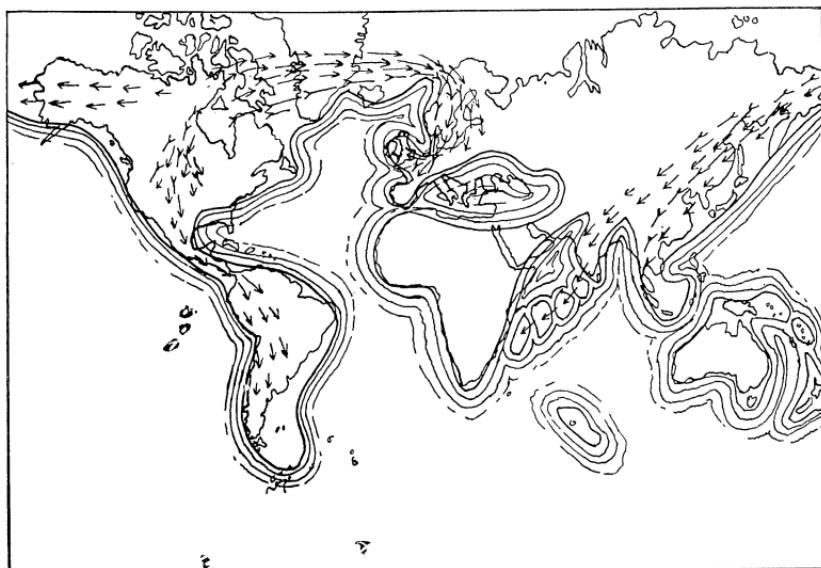
THE development of the primates has taken place in regions of comparatively high temperatures, especially in tropical and semitropical climate. This is chiefly due to their arboreal adaptation, which keeps them where the trees throughout the year offer food either as fruit, leaves, blossoms, insects or small animals.

The first primates are yet to be found, but they doubtless lived either during the last of the Cretaceous or in the earliest Eocene; for during the Lower Eocene of the Wasatch epoch there suddenly appear in America two well-distinguished families of primates, the general feeders or Notharctidæ, and the fruit eaters or Anaptomorphidæ.¹ Between these no intermediate or ancestral group is known, but the wide divergence in form would indicate a considerable time element for development. The genera *Anaptomorphus* and *Pelycodus* appear in America as a part of the wave of migration which introduces for the first time representatives of the modern groups of mammals. Somewhat later the primates appear in England and France, apparently part of the same original stock but differing slightly as a result of independent development.

The original group of primates or ancestral stock seems to have been a large-brained arboreal insectivore, somewhat similar to the tree shrews (*Tupaiidæ*). Apparently their home was to the north in the Hudson Bay

¹ The considerable group termed Proglires by Osborn and including *Mixodectes*, *Microsyops*, *Cynodontomys*, *Indrodon*, *Olbodotes*, etc., all having in common the gnawing adaptation and a very primate-like set of premolars and molars, are now assigned by Matthew and Osborn to the Insectivora.

region or further north in the forest areas; and under the decidedly tropical climate which is evidenced by the palms and ferns, crocodiles and primates themselves.² From this ancestral center the first primates, along with other groups, migrated in all directions possible, climate and land bridges being considered. This opened three paths, one south into America, a second southeasterly into England and France, and a third southwesterly into Asia, thence ever southerly across China and India and along the Indo-Madagascar isthmus (or chain of islands) to Madagascar and Africa.



→ General Feeders ↘ Fruit Eaters
FIG. 1. Diagram of the radiation of the primates in the Eocene.

The first primates, as indicated, separate into two groups, first a group of long-headed (dolicocephalic) general feeders with unspecialized teeth, which probably took fruit, leaves, insects and small animals: and second a group of short headed (brachycephalic) fruit-eaters with crowded and rather high pointed teeth. These are

² For a discussion of the climate see Wortman, *Amer. Jour. Sci.*, 1903, Vol. 165, p. 417; and Wieland, same journal, Vol. 166, p. 401, 1903.

the first adaptations of the primates and it probably took some time to arrive at the degree of difference found in the Wasatch of North America.

The fruit-eating brachycephalic group includes *Anaptomorphus* of American Eocene, *Necrolemur* and *Microchærus* of the European Eocene, and *Tarsius*, now living in southeast Asia. During the Eocene the climate was progressively colder, becoming at least temperate by the

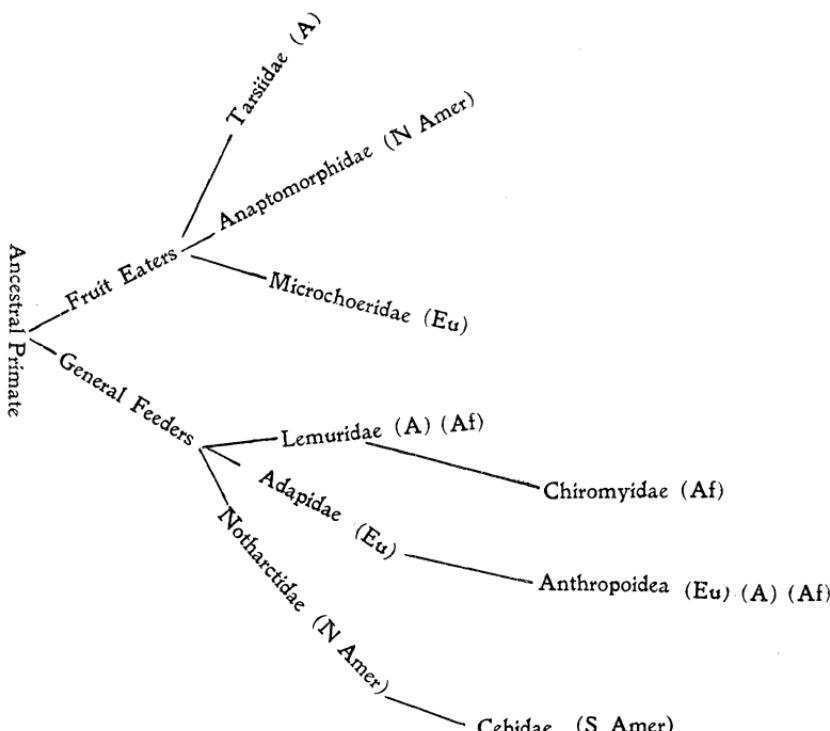


FIG. 2. Genealogical relationships of the Eocene primates.

end of the Eocene in the northern parts of America. This climate acted to force southward all the primates of the north and also several other groups, so that during the Lower Eocene we have the whole primate group pushing down, the Anaptomorphidae all over North America, the Microchoeridae on to what there was of Europe and the ancestors of *Tarsius*³ on to eastern Asia,

³ Earle, AMER. NAT., Vol. 31, pp. 569-575 and 680-689, 1897.

which through the lower and middle Eocene was separated from Europe. The fact that *Tarsius* is confined to islands possibly explains why it has remained in so primitive a condition in many ways, though specialized in the limbs which are as yet unknown in any others of this group.

The general feeders are a larger and more abundantly preserved group. It includes the *Notharctidæ*⁴ of North America (to which belong *Pelycodus* and *Notharctus*) ; the *Adapiidæ* of Europe⁵ (including *Adapis* and *Plesadapis*) ; the *Homunculidæ*⁶ of South American Miocene (including the genera *Homunculus*, *Pitheculites*, *Homunculites*) and lastly the living lemurs of southern Asia, Madagascar and Africa. All have the dentition $\frac{2}{2}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{3}{3} = 40$, and long heads, and apparently ate both vegetable and animal food. The group originated like the foregoing in northern America and migrated southward, driven by the change in climate. The earliest known forms are those in the Wasatch of western America, and they are likewise the most primitive. Though preserved only in Wyoming and New Mexico, they probably occupied pretty much all of our western plains country, then forested. South America seems to have been isolated from early Eocene times, so that some representatives of this group probably got into that continent by early Eocene times, *i. e.*, the radiation over North America must have been pretty rapid and general by lower Eocene times. Those in North America after the separation of South America flourished for some time, being especially abundant in the Wind River and Bridger epochs, but with the cold of the Uinta epoch they were crowded south and finally exterminated in North America, never more to be widely distributed on that continent.

⁴ See Osborn, *Bull. Amer. Museum Nat. Hist.*, Vol. 16, pp. 169–214, 1902, except *Hyopsodontidæ*; and Loomis, *Amer. Jour. Sci.*, Vol. 171, pp. 277–285, 1906.

⁵ See Schlosser, “Die Affen, Lemuren, Chiropteren, etc.,” des Europäischen Tertiärs, Theil 1, s. 19–54, 1887.

⁶ See Ameghino, *Anal. d. Museo Nac. d. Buenos Aires*, Vol. 15, pp. 424–429, 1906.

Those in South America quickly differentiated by the loss of the first premolar, making a dental formula of $\frac{2}{2}, \frac{1}{1}, \frac{3}{3}, \frac{3}{3} = 36$. With this also goes a deepening of the ramus of the lower jaw, a shortening of the face, and a tendency to develop the occipital region so that it overhangs widely the foramen magnum. This group of forms is termed the Cebidæ. On becoming successfully adapted to the South American continent and during the long isolation of that area, these early forms have gradually adapted themselves in various directions, often paralleling old world types. In size they have developed, the largest forms having a body of 27 to 28 inches in length, and legs as long, making a height of $4\frac{1}{2}$ feet, which is a good-sized monkey. They have always remained arboreal with opposable thumbs and a prehensile tail; but they vary from the slender spider monkeys to the robust and powerful woolly monkeys (*Lagothrix*). From the above has been specialized the family of marmosets (Hapalidæ), by the loss of the last molar (making the dentition $\frac{2}{2}, \frac{1}{1}, \frac{3}{3}, \frac{2}{2} = 32$), by the development of a broad nasal septum, the loss of the prehensile character of the tail and opposability of the thumb.

The southwesterly wave of migration crossed the Behring's connection and moved down the easterly part of Asia across the Indo-Madagascar isthmus and into Africa. This isthmus or series of islands sank at or toward the end of the Eocene, leaving lemurs stranded all along the area occupied by the isthmus. Those on the islands and especially on Madagascar have remained very much as they were, adapting themselves in minor ways, but being always arboreal. Some peculiarities must have developed very early for they are common to the group, like the having of the lower incisors projecting forward (proclivous), the lower canine small and like an incisor, while the first premolar acts as a canine tooth. Then the fourth digit of the hand is longest, and the second one of the foot is clawed instead of having a nail. In this lemur group we know only the immediate

ancestors of the living forms, and as yet no record has been found of the forms intermediate between those on America and the living types. In the case of the Madagascar form, *Chiromys* or the aye-aye, we have a representative of the group which has adopted a gnawing habit to get grubs, etc., under the bark, and a great change has resulted in the dentition, by which the first incisor has become specialized into a rodent-like gnawing tooth and there is a reduction in the teeth so that the formula is only $\frac{1}{1}$, $\frac{0}{0}$, $\frac{1}{0}$, $\frac{3}{3}=18$.

The easterly wave of migration is represented by several species of *Adapis* found in the middle and upper Eocene of England and France. Apparently the progress of this easterly migration was slower, so that they reach Europe considerably later than the same latitude in America. The primates are not in the front wave of immigration on the European side, so that it is possible that the forested condition was not as favorable. The Adapiidæ in Europe, small primates with a long low skull and the ancestral dental formula $\frac{2}{2}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{3}{3}=40$, the teeth being very generalized.

With the close of the Eocene the first adaptive radiation of the Primates was complete, and they had achieved an almost world-wide distribution. At the end of the period the North American contingent was extinct, the South American group was isolated, the Asiatic and African forms were scattered on islands and on the African continent, and the European contingent was located in central and southern Europe, or what land there was at that time in those regions (see Fig. 3); and it is among these that the next act in the great primate drama took place.

The Oligocene period is one in which there was a gradual rising or emergence of continental areas so that the southern part of Europe was an archipelago, which toward the end developed into a long peninsula, extending from the present Asia Minor (see Fig. 3). During this period the change in the Adapiidæ is but little known, but

during that time they shortened the skull and lost the first two premolars, and made a considerable increase in size. In Europe their remains are very scarce and confined to the Lower Oligocene when it was the true *Adapis* which was holding over from the Eocene. Schlosser has just reported some primates from the Fayûm formations of Oligocene age in northern Africa. These he gives new generic names, *Mærripithecus*, *Parapithecus* and *Proplopithecus*, assigning the first two to the Cercopithecidae and the last to the Simiidæ. They seem from the descriptions to be primitive members of the Cercopithecidae, which would indicate that the change to the modern type by the loss of the first two premolars was accomplished in the early Oligocene, perhaps in Africa as the two areas are in connection at the time across Gibraltar.⁷

At the beginning of the Miocene the European primates had the dental formula $\frac{2}{2}, \frac{1}{1}, \frac{2}{2}, \frac{3}{3} = 32$, a shortened face, and a shortened tail, but were still arboreal forms. During the Lower Miocene two divisions arise, the one adhering to the quadrupedal gait, the heavy jaws and longer snout: the other acquiring the bipedal gait, and shortening the face with a corresponding broadening of the teeth. In both divisions there is a tendency to come down to the ground.

The former group is the Cercopithecidae in its broad sense, or "old world monkeys"; while the latter are the Simiidæ or apes.

The Cercopithecidae seem to run back to some such form as the *Oreopithecus*, found in northern Italy, and presenting dental characteristics resembling the baboon, but at the same time having a shortened face suggesting the Simiidæ. A second form belonging to this group is *Mesopithecus* found in considerable abundance in the Lower Pliocene of Greece. This form seems to be intermediate between the macaques and langurs, resem-

⁷ For geography see Matthew, *Bull. Amer. Museum Nat. Hist.*, Vol. 22, p. 364, 1906. For the Fayum Primates, see *Zoologischen Anzeiger*, Bd. 35, for March, 1910, and Matthew, *AMER. NAT.*, Vol. 44, Nov., 1910, p. 700.

bling the former in the stout limbs, the latter in its dentition. Considering the different subfamilies it would appear that the Cercopithecidae originated in southern Europe, that it was fairly successful, and that as a result of this, the family adapted itself in three directions; first one group left the trees and took to life on the ground, giving rise to *Cynocephalus* and *Macacus*; the second group became leaf feeders, and developed a pouched stomach and for some reason also disproportionately long hind limbs, giving rise to *Semnopithecus* and *Nasalis* of Asia and *Colobus* of Africa: while those remaining in the trees and changing but little are *Cercopithecus* and *Cercocebus* of Africa.

The differentiations took place in the Miocene and are fundamentally based on food supplies. Those forms which had developed strength enough to defend themselves, their fore and hind limbs being approximately equal in length, and their food including insects, lizards, frogs, etc., as well as all sorts of vegetable life, like leaves, fruit, blossoms, etc., came down from the trees.

The terrestrial forms which continued to live in the forests make the genus *Macacus*, or macaques, which during the Pliocene spread pretty well all over Europe, even up into England, and also into western Asia where they still live. In the Pleistocene some representatives of the genus went with the great wave of migration from southern Asia into Africa, but they have become extinct in that continent except for one species, the Barbary ape. Those members of the group which left the woods and took to the more open country developed great strength and powerful jaws and are the baboons (*Cynocephalus*). These too originated in southern Europe and migrated during the Pliocene eastward into Asia, and during the Pleistocene on down into Africa, to which continent they are now confined.

The second subfamily of the Cercopithecidae are the langurs (*Semnopithecus*, *Nasalis* and *Colobus*) which, while remaining largely arboreal, have specialized as her-



→ *Cercopithecus* line

— Cynocephalus Macacus line

..... Semnopithecus line

FIG. 3. Diagram of the radiation of the quadrupedal old world monkeys.

bivors among the primates, feeding exclusively on leaves; in response to which they have developed a stomach of several pouches comparable to that of a sheep or cow. Like the preceding subfamily, they originated in southern Europe and during the Pliocene moved over into southern Asia, where the langurs and the nasal monkeys live to-day. Some members of the group, however, moved during the Pleistocene in Africa where the thumb was much reduced, which feature distinguishes the genus *Colobus*.

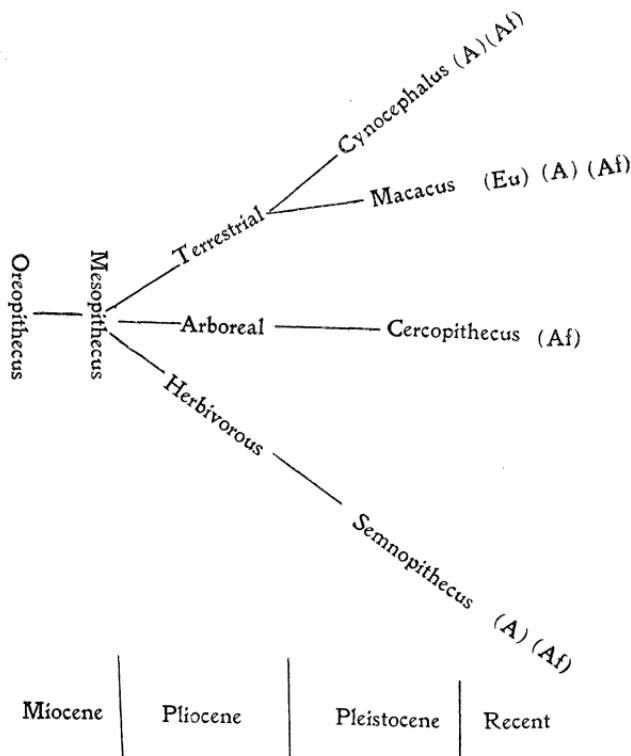


FIG. 4. Genealogical relationships of the quadrupedal old world monkeys.

Lastly the unspecialized subdivision of the family, the *Cercopithecus* genus, followed the same lines of migration and reached Africa where they now live, having spread over the major part of the continent.

Turning back to the early Miocene, we find that there

was another group of primates which tended to come to the ground, and these tended to assume a more or less upright position, with a bipedal gait. The hands thus free to take hold of objects, were free to develop a deftness and adaptability, which seems to be the key to the progressive development of the apes. It seems however that this handling of objects (food, sticks, stones) began before they left the trees and was really the cause of taking the bipedal gait. The climbing offered an ever changing grasp and carrying food to the mouth was a natural starting point; so that, with the front paws used as hands, there is a good reason for exempting them from the heavy work of locomotion. Contributory to this idea is the eolith development. These crude flaked flints⁸ begin back in the Miocene at least, and as Penck⁹ suggests the only known primate which might be suggested as an eolith-maker is *Dryopithecus*. It seems highly probable then that the hands had begun to be used as such before the first apes came to the ground and that this specialization of the hand was the cause of the upright position and bipedal gait. Of course the varied experience resulting from taking up all sorts of objects and using them for different purposes tended to develop the intelligence, and that furthered handling, the two acting and reacting on each other.

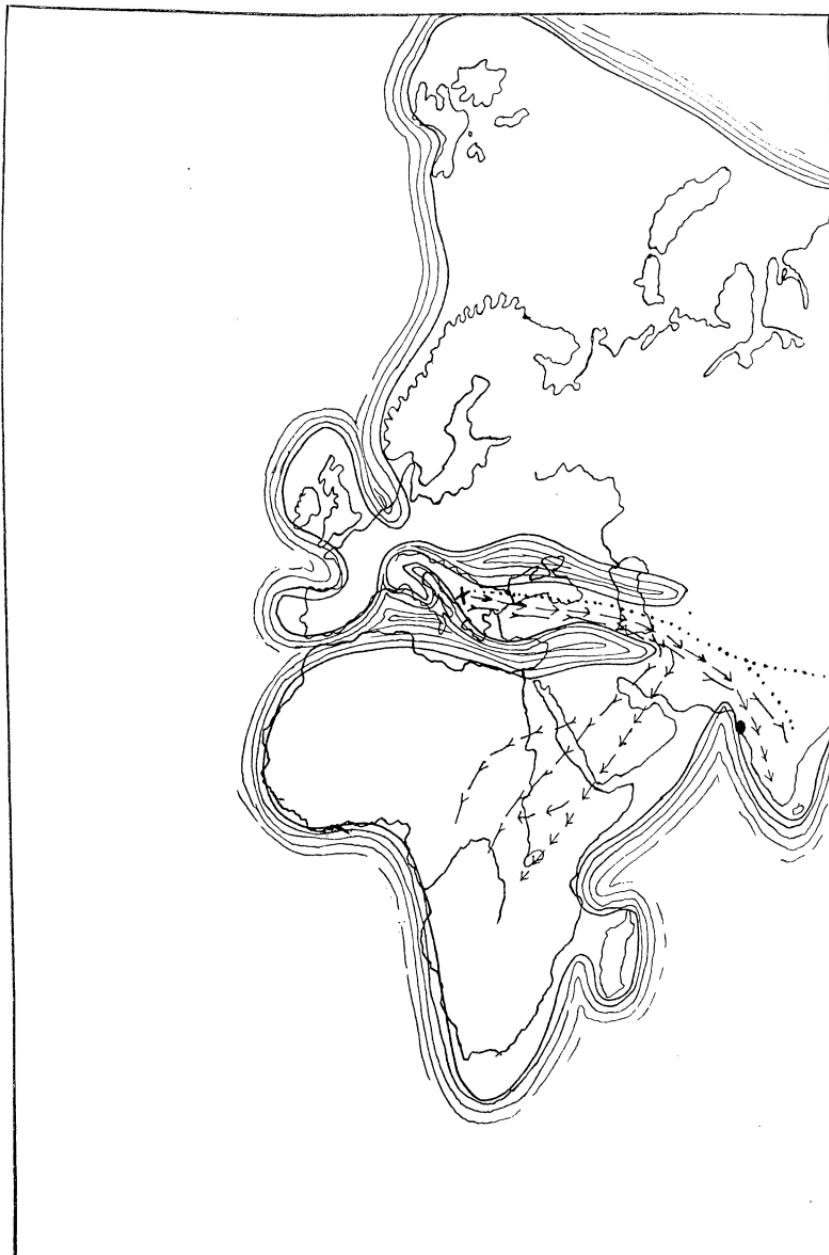
In the early Pliocene of southern Europe three divisions of the simian group have already arisen,¹⁰ one group remaining arboreal, or more probably reverting again to the trees, a second group developing great muscular and skeletal strength, the third group developing especially the brain and central nervous system.

The first of these groups, *i. e.*, the retrogressive or aboreal group, is represented in the Upper Miocene of southern Europe by *Pliopithecus*, a form ancestral to the modern gibbons, and one which during the upper Miocene

⁸ See MacCurdy, *Amer. Anthropol.*, Vol. 7, n. s., pp. 425-479, 1905.

⁹ *Science*, Vol. 29, n. s., p. 359, 1909.

¹⁰ See Schlosser, *Zoologischen Anzeiger*, Vol. 22, p. 289, 1900.



→ *Anthropithecus* → *Gorilla Simia* *Hylobates*
line to *Man*

FIG. 5. Diagram of the radiations of the bipedal primates or apes.

and lower Pliocene spread over a large part of Europe (France, Germany, Switzerland). However when the colder climate of the Pliocene developed, the European contingent was exterminated, and only those in Asia have survived as the gibbons of to-day.

The second group which developed especially strength is rare both in prehistoric and recent times: but it seems

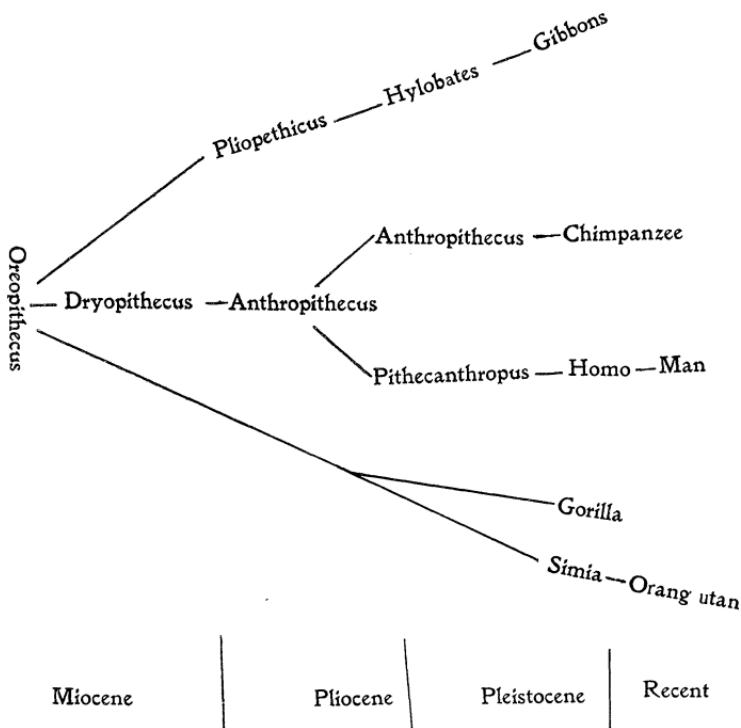


FIG. 6. Genealogical relationships of the anthropoid apes.

to have originated first in southern Europe though no representatives have yet been found. In the Pliocene however the genus *Simia* has been found in southern Asia where its representatives still remain as the orang utan. During the Pleistocene representatives of the group seem to have reached Africa where they have persisted as the gorilla.

The third group has at its base *Dryopithecus*, the middle and upper Miocene ape which ranged over a con-

siderable part of Europe: but at the end of the Miocene this form became extinct and with it the last of the chimpanzee line in Europe, the next representative being *Anthropithecus*, the true chimpanzees, found in the Pliocene of India. This first chimpanzee makes a slightly closer approximation to man than the living species. During the Pleistocene the wave of immigration into Africa included *Anthropithecus*, which has survived only on that continent. In 1896 Dubois found in Java in beds now generally called early Pleistocene, the top of a skull, a femur, and a few fragments of a transitional form which is in many ways like the apes and in others like man. This he called *Pithecanthropus erectus*, and it stands as either a very high grade ape or as a low grade man, the latter being the usual designation. If not the actual ancestor of man, it is at least a typical stage in his development.

From the distribution of *Anthropithecus* and *Pithecanthropus* it seems certain that man originated in southern Asia, at least by the beginning of the Pleistocene: and that he radiated from there westward across Europe where such remains as the Heidelberg jaw, and those of the Neanderthal type have been found so widely. He probably also migrated easterly into North America, and thence south with the Pleistocene fauna into South America where very primitive remains have recently been described by Ameghino as *Diprothomo platensis*, and *Homo pampensis*. Remains have been strangely scarce in North America, though the fauna, with which early man usually associated is present in various parts of the continent.